

NOMENCLATURE AND BIOLOGY OF *ASTRANGIA POCULATA*
(=*A. DANAЕ*, =*A. ASTREIFORMIS*)
(CNIDARIA: ANTHOZOA)

Esther C. Peters, Stephen D. Cairns, Michael E. Q. Pilson, John W. Wells,
Walter C. Jaap, Judith C. Lang, Carol E. (Cummings) Vasleski, and
Lauren St. Pierre Gollahon

Abstract.—The encrusting to ramose northern star coral, *Astrangia poculata*, is a common inhabitant of rocky shorelines, jetties, and pilings along the north-west Atlantic and Gulf of Mexico coastlines of the United States. Despite its popularity as an experimental laboratory animal, there has been considerable confusion as to the number of species which may exist and the proper name(s) of the species. A reexamination of material from throughout this range confirms that there is only one species, the correct name of which is *Astrangia poculata* (Ellis & Solander, 1786). A neotype has been deposited in the National Museum of Natural History. The same neotype is also deposited as the type of *A. michelinii* Milne Edwards & Haime 1849, type species of *Astrangia*.

The genus *Astrangia* includes over 30 Recent nominal species within the family Rhizangiidae, and is represented by 20 fossil species, some of which lived as early as the Middle Cretaceous, approximately 100 million years ago (Wells 1956). Members of the genus are all relatively small and are usually insignificant components of the fauna where they occur. The various species of *Astrangia*, however, collectively occupy a vast geographic range, possibly broader than that of any other genus of coral.

Unfortunately, the genus *Astrangia* has never been completely reviewed. It is probable that many species names are synonyms, and also that a number of yet undiscovered species may exist (Pilson 1975). The confusion that exists within this genus became evident when a group of scientists at the University of Rhode Island began a series of studies on the ecology, physiology, and life history of the coral found in Narragansett Bay. Whereas several previous studies had referred to the northern star coral as *Astrangia danae*, a number of other papers had been published on the very sim-

ilar *Astrangia astreiformis* from the southeastern coasts of the United States. However, other texts suggested that only one species of *Astrangia* existed along the entire North Atlantic and Gulf coasts of North America (Hyman 1940, Wells 1956, for reviews see Cummings 1983, and Jaap, in prep.). *A. astreiformis* was also reported to occur off the west coast of Africa (Thiel 1928, Chevalier 1966).

Throughout its range, the northern star coral appears remarkably tolerant of a wide range of environmental conditions. Colonies of *Astrangia* are generally considered to be ahermatypic (non-reef-building) and hence azooxanthellate (=asymbiotic, i.e., lacking zooxanthellae), but some colonies of the northern star coral contain these algal cells abundantly within their tissues (Boschma 1925a). These two factors, adaptability and variability in algal symbiosis, have contributed to the increasing popularity of this coral as an experimental laboratory animal. Therefore, in order to aid future researchers, we were motivated to clarify the taxonomic status of this coral.

Family Rhizangiidae d'Orbigny, 1851

Genus *Astrangia* Milne Edwards
& Haime, 1848a

Diagnosis.—Colonial, usually azooxanthellate. Colonies encrusting or subplocoid, formed by extratentacular budding from edge zone; corallites united basally by thin coenosteum; septa dentate; columella papillary. [Type species: *A. michelinii* Milne Edwards & Haime, 1848b, by monotypy (= *A. poculata* Ellis & Solander, 1786).]

Astrangia poculata
(Ellis & Solander, 1786)
Figs. 1–6

“Stony coral found on the shore near New York.”: Ellis, 1755:84, pl. 32, figs. A. 1, A. 3.

?*Madrepora calycularis* Pallas, var. β , 1766: 319 note 186B.—Esper, 1790:283.

Madrepora poculata Ellis & Solander, 1786: 165.—Gmélín, 1791:3766.—Esper, 1790: 283 (= *M. calycularis* β). [Original type locality “near New York.” Type specimen lost (P. F. S. Cornelius, pers. comm.). Type locality (neotype) “off Atlantic City, New Jersey.” Neotype deposited in the National Museum of Natural History USNM 80350.]

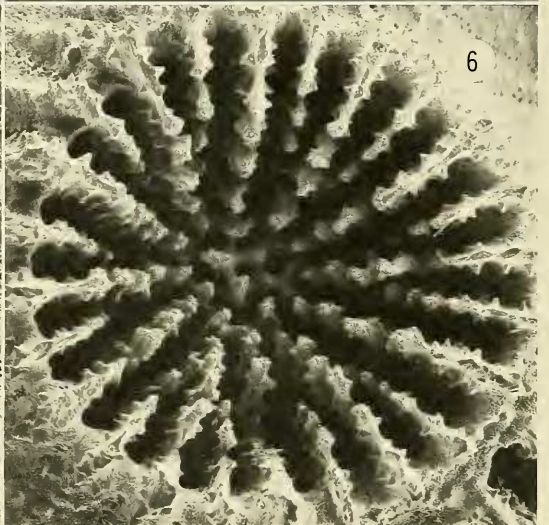
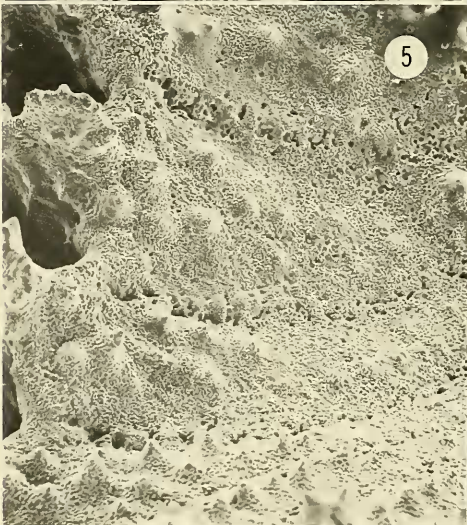
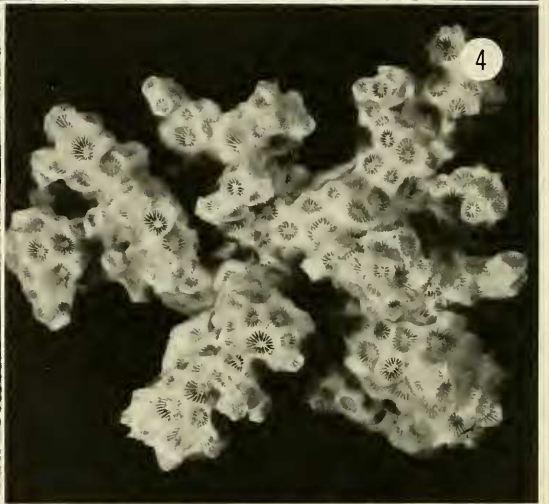
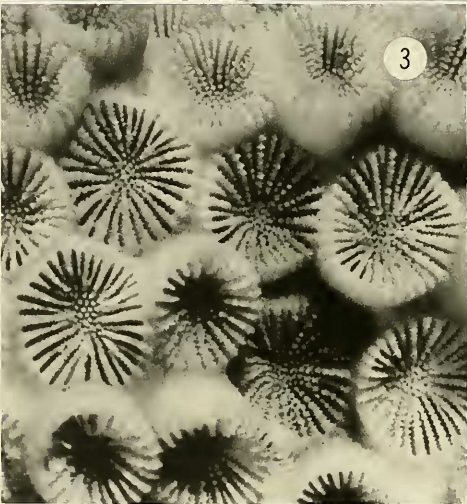
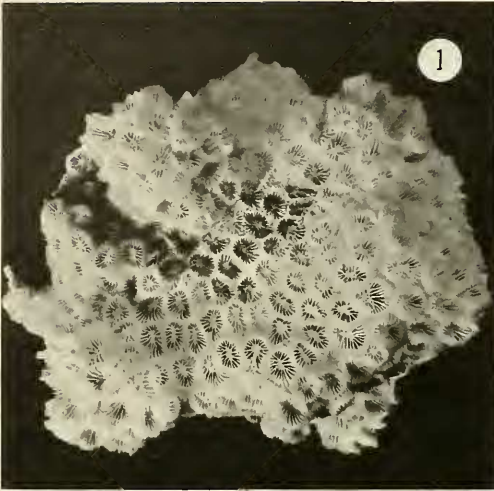
Madrepora porculata: Turton, 1806:623 [Misspelling of *poculata*].

Astrangia michelinii Milne Edwards & Haime (ME & H), 1848b:320, pl. 7, fig. 5, 5a; 1857:614. [Type of the genus. Original type locality unknown. Type specimen last seen by Wells in 1934, Coll. Michelin No. 412. Type lost (Chevalier, 1966). Type locality (neotype) “off Atlantic City, New Jersey.” Neotype deposited in the USNM, USNM 80350.]

Astrangia michelini: ME & H, 1849:181; 1850:xliv (cited as the type species).—Verrill, 1866a:324.—Vaughan, 1901: 299.—Vaughan & Wells, 1943:177.—Alloiteau, 1952:623 (= *A. danae* Agassiz 1850).—Chevalier, 1966:930 (= ?*A. astraeiformis* ME & H 1849).—Wells,

1986:6 (cited as the type species). [Emended spelling of *A. michelinii*.]
Astrangia danae ME & H, 1849:180.—Verrill, 1863:40; 1864:47 (not *A. danae* Agassiz 1850); 1866a:324 (= *A. edwardsii*); 1866b:335; 1872:432–438; 1874:446 (geography).—Pearse & Wharton, 1938: 636.—Cairns, 1979:207.—Jacques & Pilson, 1980:167–178 (physiology, symbionts, Rhode Island).—Szmant-Froelich, 1980a:1–191 (natural history, biochemistry, Rhode Island).—Szmant-Froelich & Pilson, 1980:85–97 (feeding frequency, biochemistry, Rhode Island).—Szmant-Froelich, 1981:133–144 (nutrition, Rhode Island).—Cummings, 1983:1–147 (physiology, morphology, Rhode Island, Florida).—Peters, 1984:61–63, figs. 6b, c, d, 10d, e, 13g, 17a, b, 22h, 26f, g (histology, Rhode Island).—Wiseman, 1984:1–75 (biochemistry).—Peters & Pilson, 1985:215–230 (sedimentation stress, histopathology, Rhode Island). [Type locality unknown. Type specimen last seen by Wells in 1934, now missing from Coll. Michelin (Cairns 1981).]

Astrangia astraeiformis ME & H, 1849:181.—Verrill, 1864:47; 1866a:324.—Vaughan, 1901:300, pl. II, figs. 2, 2a, 2b (Puerto Rico).—Whitten et al., 1950:75 (Texas channels).—Parker, 1959:2130, 2131, fig. 19a; 1960:317, 334, pl. 3, fig. 23 (inlet and deep channel assemblage, common on shell, Texas).—Richmond, 1962:69 (Mississippi).—Wells et al., 1964:566, 581 (on scallop shells, North Carolina).—Macintyre & Pilkey, 1969:374–375 (off North Carolina).—Macintyre, 1970: 178.—Pampe, 1971:399, pl. 2, fig. 7.—Defenbaugh, 1976:27, 37, pl. 5f, fig. 53.—Cairns, 1977:5; 1978:10 (east, west and southwestern Gulf of Mexico, 10–29 m); 1981:10, fig. 12 (systematics: = *A. danae* Agassiz 1850 not *A. danae* ME & H 1849).—Cooley, 1978:8, 86 (Pensacola, Florida, estuary).—Fotheringham et al., 1980:17, 103, fig. 2.25.—Brunet, 1982:1–150 (feeding behavior, growth and sur-



- vival, Texas).—St. Pierre, 1986:1–55 (reproduction, Texas). [Type locality “United States.” Type found by Wells in Paris in Coll. Michelin in 1934, but not found by Chevalier in 1980 (Cairns 1981).]
- Astrangia danae* Agassiz, 1850:68–77, pl. I, fig. 7 (feeding behavior, digestion, colony growth, new polyp formation, nematocyst function, Massachusetts).—Verrill, 1863:40 (North Carolina); 1864:47 (= *A. astreiformis* in Leidy, 1855, not *A. danae* ME & H 1849); 1866a:324 (not *A. danae* ME & H 1849); 1866b:335; 1872:436, 437 (= *A. astreiformis* ME & H 1849); 1873:408; 1874:446 (Vineyard Sound and adjacent waters).—Agassiz & Agassiz, 1865:16, figs. 16–20.—Pourtalès, 1871:80.—Dana, 1872, 1890:67–68, figured p. 68, a, b, c.—Damon, 1882:221.—Fewkes, 1889:7–10, pls. 1–5 (natural history illustrations); 1891:53.—Hargitt, 1914:250, pl. 43, fig. 9 (natural history, Casco Bay, Maine).—Boschma, 1925a:65–67 (zooxanthellae symbiosis); 1925b:407–439 (feeding behavior, digestion, zooxanthellae symbiosis).—Cowles, 1930:333 (Chesapeake Bay, Cape Henry, Cape Charles).—Pratt, 1935:159, fig. 239.—Pearse, 1936:178.—Richards & Harbison, 1942:178, pl. 22, figs. 2 & 3 (Miocene, New Jersey).—Vaughan & Wells, 1943:177 (see footnote 52: =? *A. michelini* ME & H 1848).—Field, 1949:6, 18, pl. I, fig. 7.—Waterman, 1950:127–131, fig. pp. 120–121 (structure of corallum and polyps, zooxanthellae, feeding, reproduction).—Alloiteau, 1952:623, fig. 74 (= *A. michelini* ME & H 1848).—Hand, 1964:25, pl. 3, fig. 4 (description).—Driscoll, 1967:633–641.—Robertson et al., 1970:55–65.—Calder, 1972:101 (Chesapeake Bay, Hog Island and Eastern Shore).—Sassaman & Mangum, 1973:1313–1319 (anaerobic metabolism).—Jacques et al., 1977:455–461 (physiology, calcification, Rhode Island).—Hayes & Goreau, 1977:26–40 (calcification, histology).—Bachand, 1978:283–284 (habitat, life history).—Calder & Hester, 1978:93 (Charleston, South Carolina).—Weston, 1980:1–93 (zooxanthellae distribution, Chesapeake Bay). [Type locality “Massachusetts.” Deposition unknown.]
- Astrangia astraiformis*: ME & H: Leidy, 1855:139–140, pl. 10, figs. 9–16 (synonymy, nematocysts, Rhode Island). [Misspelling of *A. astreiformis* ME & H 1849].
- Astrangia astraeiformis*: ME & H: ME & H, 1857:614.—Verrill, 1863:39; 1866a:324; 1866b:335; 1872:436 (= *A. danae* Agassiz 1850).—Pourtalès, 1871:80.—not Thiel, 1928:283–285, pl. 2, fig. 22 (= *A. mercatoris* Thiel 1941, West Coast of Africa).—Thiel, 1941:5, 15, pl. 1, figs. 5–6 (Martinique).—Pearse & Williams, 1951:136 (incorrectly attributed to Leidy, 1855, Maine to Florida and the West Indies).—Chevalier, 1966:926–930, pl. 3, figs. 2–3, pl. 4, fig. 6 (synonymy, description, Sierra Leone, Africa). [Misspelling (or corrected spelling) of *A. astreiformis* ME & H 1849.]
- Astrangia danai*: ME & H, 1857:614. [Misspelling (or corrected gender) of *A. danae* ME & H 1849.]
- Astrangia edwardsii* Verrill, 1866a:324 (=nom. nov. for *A. danae* ME & H 1849, see Remarks); 1866b:335.
- not *Astrangia mercatoris* Thiel, 1941:16–17, pl. 2, fig. 1 (= *A. astraeiformis* Thiel, 1928:283–285, pl. 2, fig. 22; Angola, Bay of Elephants, West Coast of Africa).—

←

Figs. 1–6. *Astrangia poculata*: 1, Neotype colony (off Atlantic City, New Jersey, USNM 80350), $\times 0.88$; 2–3, Colony from off Jacksonville, Florida, 15 m, USNM 78509, $\times 1.20$, $\times 3.40$, respectively; 4, Deep-water branched colony (off Western Dry Rocks, Sand Key, Florida, 263 m, USNM 78508), $\times 0.86$; 5, SEM of coenosteum adjacent to calice showing lines of perforations constituting intercostal striae and coenosteal granules, $\times 49$; 6, SEM of calice with 24 septa, $\times 23$ (5–6, R/V Gerda station 1002, USNM 78507).

- Chevalier, 1966:929–930 (discusses synonymy, see Remarks).
- Astrangia astraeiformis*: no authority cited: Hedgpeth, 1953:164 (Texas). [Misspelling of *A. astreiformis*.]
- not *Astrangia astraeiformis*: no authority cited: Buchanan, 1954:85–86 (= *A. astraeiformis* Thiel 1928 = *A. mercatoris* Thiel 1941, Ivory Coast, French Congo, Angola, Africa). [Misspelling of *A. astreiformis*.]
- Astrangea danae*: no authority cited: Goreau & Bowen, 1955:1188 (calcification). [Misspelling of *Astrangia danae*.]
- Astrangia astreiformis*: Milne Edwards & Haines (sic): Pampe, 1971:399, pl. 2, fig. 7 (Pleistocene, Texas). [Misspelling, spelled *A. astreiformis* later on same page.]
- Astrangia asteriformis*: no authority cited: Rudloe, 1971:154–157, 167, 172–174, figured on p. 174 (natural history, hardness in aquarium, Florida). [Misspelling.]
- Astrangia astreiformis*: no authority cited: Ladd, 1951:137, 139, 149 (Texas coastal waters).—Stephenson & Stephenson, 1952:35 (distribution, taxonomy).—Hedgpeth, 1953:164 (Texas).—Gunter & Geyer, 1955:40, 44, 45, 56, 57, 65 (Texas, Louisiana).—Parker, 1956:310, 315, 329, 354, 370 (dead specimens collected in east Mississippi delta region).—Courtney & Edmond, 1974:63 (Marco Island, Florida).—Fotheringham & Brunenmeister, 1975:36, 161, fig. 2.24 (natural history).
- Astrangia danae*: no authority cited: Wilson, 1900:350 (North Carolina).—Allee, 1923:176 (Woods Hole, Buzzards Bay, and Vineyard Sound, Massachusetts).—Hyman, 1940:610–611 (morphology, natural history).—Storer, 1951, figured on p. 321.—Stephenson & Stephenson, 1952:35 (distribution, taxonomy).—Blake, 1953:23 (Pleistocene, Maryland).—Zinn, 1964:15 (Rhode Island).—Goreau et al., 1971:254.—Williams & Murdoch, 1973:551–563 (effects of gamma radiation on).—Cummings, 1976:1–115 (physiology, Rhode Island).—Szmant-Froelich & Pilson, 1977:417–424 (nitrogen excretion, symbiosis, Rhode Island).—Hoffman et al., 1978:165–170.—Jacques, 1978:1–169 (calcification).—Gosner, 1979:93–94, fig. 20.—Storer et al., 1979, figured on p. 320, 372, 390.—Szmant-Froelich, 1980b:1–3 (popular account).—Szmant-Froelich et al., 1980:257–269 (reproduction, Rhode Island).—Meinkoth, 1981:391.—Cummings & McCarty, 1982:1125–1129 (calcification, stable carbon isotopes, Rhode Island).—Jacques et al., 1983:135–148 (ecology, metabolism, Rhode Island).—Swart, 1983:72 (stable carbon isotopes).—Szmant-Froelich & Pilson, 1984:153–162 (feeding frequency, nitrogen metabolism, respiration, Rhode Island).
- Astrangia* sp.: Ferguson, 1948:17 (salinity tolerance, Louisiana).—Keith & Weber, 1965:500 (isotopic composition, calcification, in part: Woods Hole, Massachusetts).—not Rabalais, 1978:62 (= *Oculina diffusa*, Gulf of Mexico).
- Diagnosis*.—Encrusting, massive, or ramose irregularly shaped colonies. Corallum cerioid to plocoid, new polyps produced by extratentacular budding, having corallites united basally by thin peritheca (vesicular coenosteum). Corallites round, irregular, or polygonal; tightly packed or spaced several millimeters apart, highly variable even within a single specimen. Calices 1–7 mm in diameter, with distinct equal costae on many corallites. Septa hexamerally arranged in 4 cycles, however, complete fourth cycle (48 septa) only attained in very large calices. Most calices have 24 septa, the S_3 merging basally with the S_2 about $\frac{3}{4}$ distance to columella. With increase in calicular diameter, pairs of S_4 form flanking some S_3 , often with one pair per system (the space between two S_1) resulting in 36 septa. Complete fourth cycle (48 septa) attained only in calices over 6 mm in diameter. Septa

strongly dentate, particularly S_3 at region of S_4 fusion, and slope gradually toward columella. Fossa shallow. Columella trabecular or papillose.

Polyps up to 1 cm tall and translucent white (azooxanthellate = asymbiotic) to brown (zooxanthellate = symbiotic, see Schuhmacher & Zibrowius 1985, for review of this terminology). Numerous nematocyst batteries on surface of tentacles; tip of tentacle rounded. Directive mesenteries present. Corallum often invaded by endolithic red or green boring algae, burrowing polychaetes, or sponges (e.g., *Cliona celata* Grant, see Cummings 1983).

Cnidocyst batteries principally composed of spirocysts. Terminal knob packed with large microbasic-p-mastigophore nematocysts (about $29\ \mu\text{m}$ long \times $8\ \mu\text{m}$ in diameter in fixed, paraffin embedded sections) and spirocysts. Occasional small microbasic-p-mastigophores scattered in epidermis (about $20\ \mu\text{m}$ long \times $7\ \mu\text{m}$ in diameter). Cnidoglandular band of mesenterial filaments possesses large microbasic-p-mastigophores (about $40\ \mu\text{m}$ long \times $7\ \mu\text{m}$ in diameter), holotrichous isorhizas (about $45\ \mu\text{m}$ long \times $15\ \mu\text{m}$ in diameter), and small microbasic mastigophores (?) (about $11\ \mu\text{m}$ long \times $5\ \mu\text{m}$ in diameter). The distribution of these nematocysts varies with location on the filament (ECP, unpublished). Histologically distinguished by well-developed longitudinal retractor muscles along the mesogleal pleats. Gastrodermis lining calicoblastic epidermis features large cells with basophilic globules (osmiophilic, non-PAS positive, non-mucin) up to $4\ \mu\text{m}$ in diameter, which increase in number and density towards base of the polyps. Calicoblastic epidermis thickened with fine eosinophilic granules (Peters 1984). Colonies gonochoric (=dioecious), gametes spawned annually (Szmant-Froelich et al. 1980, St. Pierre 1986).

Remarks.—*Madrepora poculata* was described by Ellis & Solander (1786), based on the illustration of a specimen from “near

New York” figured by Ellis (1755). Another reference to this “American” coral appeared in Pallas (1766) under the name *Madrepora calycularis*, var. β . Typical *M. calycularis* Pallas (1766) is now known as *Astroides calycularis* (Pallas, 1766), found only in the Mediterranean (Zibrowius 1980). Therefore, the name *calycularis*, even if applied to a specimen of western Atlantic *Astrangia* as form β , is preoccupied by the Mediterranean species. Esper (1790:283) equated *M. poculata* with the *M. calycularis* β of Pallas, describing a corallum encrusting an American gastropod, which may have been the same as the astrangid-encrusted specimen of *Conus spurius* from the West Indies, figured by Seba (1758:152, pl. 55, figs. 11, 12). The last known reference to *M. poculata* was Turton (1806).

ME & H (1848b) described *Astrangia michelini* as an illustration found in Memoire 4, Monographie des Astreides; this is a valid “indication” (International Code of Zoological Nomenclature (ICZN) 1985: Article 16, vii), and therefore it is a valid species and the type species of *Astrangia* by monotypy. It was described without a type locality.

In 1849, ME & H described (in order) 3 types in the Muséum National d’Histoire Naturelle, Paris, (MNHN), *Astrangia danae*, *Astrangia michelini*, and *Astrangia astreiformis*. The descriptions of the type specimens were very similar. They noted that *A. michelini* was closely related to *A. danae*. Unfortunately, only the type locality of one of the 3 species, *A. astreiformis*, was given, as from the “United States.”

Agassiz (1850) described the same species from the United States and used one of the same names used by ME & H, *Astrangia danae*, in a paper presented before the American Association for the Advancement of Science meeting in 1849, but it was not published until 1850. He made no comparisons and apparently did not know that the name had already been used for a species in the previous year (ME & H 1849), and

therefore was a junior primary homonym. It is curious that Dana (1872, 1890) referred to *A. danae* Agassiz, suggesting that he had not been in correspondence with ME & H in the late 1800's. Dana noted that he himself had proposed the name *Pleiadia* for the genus, alluding to the crowd of stars (the appearance of the corallum), in his report on Zoophytes (Dana 1846:722, Wells 1986: 50, nom. nud.). However, Agassiz (1850: 69) made no reference to this particular report. That he chose to call his species *Astrangia* presumably means that he had seen the figure (if not the specimen on one of his European trips) of *A. michelinii* published in 1848.

Later authors, who had compared the type specimens and descriptions, commented on the relations of these species. Vaughan (1901:300) noted that the specimen of *Astrangia astreiformis* (corallites free above their bases), which he had collected in Puerto Rico, was not typical of the specimens of *A. astreiformis* then in the USNM, and observed that the figure of *A. michelini* ME & H "suggests great similarity to the specimen from Puerto Rico." Alloiteau (1952) believed that *A. michelini* ME & H was the same species as *A. danae* Agassiz. Chevalier (1966) observed that *A. astraeiformis* ME & H was similar to *A. michelini* of ME & H. Thus, *A. michelinii* Milne Edwards & Haime is "similar" to *A. danae* Agassiz (Vaughan & Wells 1943, Alloiteau 1952), *A. astreiformis* ME & H (Vaughan 1901, Chevalier 1966), and *A. danae* ME & H (Milne Edwards & Haime 1849).

Leidy (1855) considered *Astrangia astreiformis* ME & H to be the same as *A. danae* Agassiz. In 1863, Verrill recorded that *A. danae* Agassiz was equal to the *A. astreiformis* described by Leidy in 1855, and noted that *A. danae* Agassiz was not the same as *A. danae* ME & H. Verrill (1866a) reported that *A. bella* E. & H. [ME & H], known from the Miocene formations in Maryland, was very similar to both *A. danae* Agassiz and *A. astreiformis* ME & H, and

noted that some authors would unite all three species. Pourtalès (1871:80) remarked "The differences between these two species (*A. astreiformis* M. E. & H. and *A. danae* Ag.) are of the slightest character, being chiefly derived from the mode of grouping, which is denser in the first than in the second. I am strongly inclined to believe that they will ultimately be united." In 1872, Verrill united *A. astreiformis* ME & H with *A. danae* Agassiz. Cummings (1983) and Jaap (in prep.) united *A. astreiformis* ME & H with *A. danae* Agassiz, noting the great variability in specimens collected from throughout its range along the coastline of the eastern United States. Only Vaughan (1901) felt that there were sufficient distinctions based on the skeletal structures to maintain *A. astreiformis* ME & H and *A. danae* Agassiz as separate species.

Thus, these observations link *Astrangia astreiformis* ME & H with *A. danae* Agassiz. Although *A. danae* ME & H appeared to be very similar to *A. astreiformis* ME & H (Leidy 1855, Chevalier 1966) and *A. michelini* ME & H (Milne Edwards & Haime 1849), subsequent authors (Verrill 1863, 1866a) did not connect *A. danae* ME & H with *A. danae* Agassiz. Verrill (1866a:324) stated again that *A. danae* ME & H ("the corallites being scattered and connected only at the base") was different from *A. danae* Agassiz, and therefore proposed the name *A. edwardsii* as a replacement name for *A. danae* ME & H. He erroneously thought that the date for Agassiz's name was 1849 and the date of ME & H's was 1850, because this latter date was cited in error by ME & H (1857:614). A number of later references attributed the publication date of Agassiz's name to 1847 (e.g., Calder 1972) or 1848 (e.g., Field 1949), further adding to the confusion. Fewkes (1889:8) noted that "The polypdom of *A. Danae* (sic) M. E. & H., is held by Prof. Joseph Leidy to be different from that of our New England species of *Astrangia* and more like *A. astraeiformis* of the same authors It is not possible to determine

from the description of *A. Danae* given by Milne Edwards & Haime whether our species differs from that which they describe under that name or not.”

J. W. Wells examined the type specimens in the MNHNP in 1934. Of *Astrangia michelini* ME & H 1848 (No. 412, Michelin Coll.), he noted “Does not look like the figure but has M.E. & H.’s label on the wooden base. Very like *A. danae* [no authority cited] except for smaller [corallites] (2.5–3.0 mm). It is attached to a bit of igneous rock. This is the type species of *Astrangia* by monotypy. No loc.” (JWW notes, February, 1934). He also observed that in the Paris collection “Specimens labeled *A. danae* [ME & H 1849] are from St. Thomas and are *A. solitaria*, coll. Duchassaing ca. 1846, *except* for one that appears to be the type. It encrusts a *Tellina* and fits the description well and is evidently conspecific with *A. michelini* as latter was figured in 1848 by M.E.&H. Has M.E.&H.’s label. No loc.” Wells noted that the type of *A. astreiformis* ME & H 1849 was in the Paris collection in 1934, with the locality designated “Etats-Unis,” but did not make any other observations on this specimen (JWW notes, February, 1934). From all indications (Cairns 1981), all of the types are now missing from the collections of the MNHNP.

Wells considered *Astrangia danae* ME & H 1849 to be the proper name for the American northern star coral (pers. comm. to A. Szmant-Froelich, 13 December 1977), noting that “Over the years I have examined many specimens from throughout this range [Massachusetts to Texas] and although there is much variation in skeletal morphology, the variation seems not be geographical or provincial, for specimens from one locality frequently show the full range of variation in compactness or isolation of corallites, size of corallites, equality of septa, etc.” Although the names *A. danae* Agassiz and *A. astreiformis* ME & H had been used nominally to separate specimens from north of Cape Hatteras to New England from those

specimens collected from south of Cape Hatteras into the eastern and western Gulf of Mexico, respectively, Wells observed that *A. danae* ME & H had priority as the senior synonym.

Cairns (1981) argued that *Astrangia astreiformis* was the appropriate name for the American species. He noted that ME & H described both *A. danae* and *A. astreiformis* in the same paper. Although *danae* had page priority, the type was lost, the description poor, and the type locality not given. He could not confirm that *A. danae* ME & H was the same as *A. danae* Agassiz and *A. astreiformis* ME & H, hence, he considered *A. danae* ME & H to be a nomen dubium. The locality for *A. astreiformis* was given as “United States.” Although the type of *A. astreiformis* was also lost, it at least had a type locality, which is why Cairns considered it as the senior synonym. Because Agassiz’s description of the same species, which he named *A. danae*, was not published until 1850, Cairns also considered this name a junior synonym of *A. astreiformis* and junior homonym of *A. danae* ME & H 1849.

Based on our present examinations of specimens and recent biological data (see below), we concur that there is only one species of star coral of the genus *Astrangia* along the Atlantic and Gulf coasts of North America. Although the type specimens are now missing from the Michelin collection, earlier observations by Leidy, Verrill, Pourtalès, Fewkes, Wells, Alloiteau, and Chevalier suggest that the *Astrangia* types established by ME & H were very similar. The latter four authors thought that these types were probably only morphological variants of the colonial northern star coral. There is no doubt that this species is the same as the *Madrepora poculata* described by Ellis & Solander over 200 years ago. Although the names *A. danae* and *A. astreiformis* have been used widely in the recent literature (73 and 41 references, respectively), these names must be considered junior subjective syn-

onyms. We conclude that the correct name, based on the Principle of Priority (ICZN 1985), is *Astrangia poculata* (Ellis & Solander, 1786).

The type specimen of *Madrepora poculata* is not present at the Glasgow or the British Museum (Natural History) and is believed to be lost (P. F. S. Cornelius, pers. comm.). In order to help clarify the complex nomenclatural issues concerning the names *Astrangia poculata*, *A. michelinii* ME & H 1848, *A. danae* ME & H 1849, *A. astreiformis* ME & H 1849, and *A. danae* Agassiz 1850, a neotype is chosen for *M. poculata*. It is deposited at the USNM (USNM 80350) and was collected from New Jersey, relatively close to the original type locality of "off New York."

As mentioned before, there is no type specimen of the type species *Astrangia michelinii* (see Chevalier 1966). Furthermore, it was described without a type locality and its original description and figures do not reliably distinguish it from the other approximately 30 Recent species in the genus. Subsequent references to *A. michelinii* have always been in its capacity as the type species of the genus, not as a new record. Therefore, in order to redefine *A. michelinii*, and the genus *Astrangia* by virtue of its status as the type species of the genus, a neotype is chosen for *A. michelinii*. Because several authors (e.g., Vaughan 1901, Alloiteau 1952, Chevalier 1966) have suggested that *A. michelinii* is synonymous with the United States east coast species, the neotype chosen for *A. michelinii* is a specimen of *A. poculata*, in fact the same specimen chosen as the neotype of *M. poculata*, a specimen from New Jersey (USNM 80350). *A. michelinii* thus becomes a junior objective synonym of *A. poculata*.

Thiel (1928) described a colonial *Astrangia* from the Atlantic coast of Africa, and identified it as *A. astraeiformis* ME & H. In 1941, Thiel doubted the existence of the American species on the west coast of Africa, and established the species *A. merca-*

toris as the African species. Buchanan (1954) reported *A. astreiformis* from the Ivory Coast and Gulf of Guinea off western Africa. Buchanan (1954:86) remarked that his specimens agreed well with Thiel's (1928) description of *A. astreiformis* from Africa. Chevalier (1966), however, believed that the American and African specimens that he examined were sufficiently similar to merit recognition as the same species. Unfortunately, as we know nothing of the African *Astrangia*, Thiel's (1928) specimens may indeed represent a different species.

Material examined.—From the USNM, 85 lots, the specimens representing the following localities: Martha's Vineyard Sound, Buzzards Bay, Woods Hole, Massachusetts; Newport, Rhode Island; 19 lots from R/V *Gosnold* collected off northeastern Florida and Georgia (13–54 m); Chesapeake Bay, Virginia Beach, Virginia; Cape Henry, North Carolina; Myrtle Beach, South Carolina; Nassau County, Florida; northeastern coast of Florida; Dry Tortugas, Western Dry Rocks off Sand Key, Florida; Marco, Gulf coast of Florida; Rockport, Galveston, Port Aransas, Texas.

Specimens from the Texas coast deposited in the Texas Memorial Museum, Austin, Texas (Numbers 1568–1573, 1753).

Specimens from the Hourglass Cruises, deposited in the collection of the Department of Natural Resources, Bureau of Marine Research, St. Petersburg, Florida (Numbers FSBC I 10027, 11360, 17984, 19858–19862) and 49 other cataloged specimens (various numbers from FSBC I 10028–31954, eastern Gulf of Mexico and Florida east coast), as well as specimens on loan from Texas A&M University (College Station, Texas), and Museum of Comparative Zoology (Harvard University, Cambridge, Massachusetts), representing locations from New England to Florida, Louisiana, and Texas.

Geologic and geographic distribution.—*Astrangia poculata* is recorded from the Miocene (Richards & Harbison 1942),

Pleistocene (Blake 1953, Pampe 1971) and Recent (Alloiteau 1952, Wells 1956). It occurs at depths from 0 to 263 m. It has been reported off Maine (Hargitt 1914) and from Cape Cod south along the eastern United States, around the Gulf coast of Florida to the southern Gulf coast of Texas and Mexico (E. Jordan pers. comm. to WCJ). It is very rare in the coastal region from south of Palm Beach to the Ten Thousand Islands, Florida, and is disjunct in the Mississippi delta region. It is also noted from Puerto Rico (Vaughan 1901) and Martinique (Thiel 1941). Thiel (1928) and Buchanan (1954) reported it from the Ivory Coast, French Congo, Angola, Africa, (although its existence off Africa based on these reports has been questioned, see Remarks), and Chevalier (1966) reported it from the Bight of Biafra, Freetown, Sierra Leone, Konakry, Guinea, Dakar and Senegal (Gulf of Guinea), Africa.

Discussion.—Coral species traditionally have been determined on the basis of their skeletal morphologies (since these are preserved most easily, and appear in the fossil record). Veron (1982) stated that biological species in corals are “the sum of a series of forms of variation which differ in relative importance from species to species.” Recent attempts to determine the range of variation which may exist within a single species have revealed the relative influence of phenotypic and genotypic variation in skeletal development, and the contributions of each may vary between species or genera (see reviews by Wijsman-Best 1974; Foster 1979, 1980). Lang (1984) reviewed the utility of non-skeletal characters to aid in the differentiation of species when skeletal characters are ambiguous or environmentally variable.

Recent studies have revealed a wide range of variation in the types of skeletal structures produced by colonies of *Astrangia poculata*. Field (1949) reported that branching forms might be found when the colonies were located in a protected spot. Cummings (1983) investigated patterns of morpholog-

ical variability in colonies of *A. poculata* from Rhode Island and the Gulf coast of Florida and found a high degree of morphologic plasticity. She noted that the parameters measured (height/length, branching, and polyp density) were correlated with exposure (light and wave action), and did not differ significantly between zooxanthellate and azooxanthellate colonies. Colonies from Panacea, Florida were, however, more branched than those from Fort Wetherill, Rhode Island, and contained more zooxanthellae per unit area of tissue. The Fort Wetherill colonies possessed more corallites per unit area and were smaller than elsewhere. As depth increased, colonies became taller and more branched, and polyp density decreased. Brunet (1982) described colonies from various sites off the Texas coast. Encrusting, mound and digitate colonies were found at the Port Aransas jetty on the channel at the end of the barrier island. Mostly mounding and a few encrusting colonies, only rarely with early digitate morphologies, were present on the pilings of the near-shore oil rigs he examined. He suggested that the digitate growth form was a response to sedimentation, to allow the polyps to extend above the substratum. He also noted that the appearance of filamentous algae growing on dead portions of the corallum might force adjacent polyps to continue growing and overtop the algae to form characteristic knobby branches. The large expansive polyps of the star coral are well-suited to removing sediment particles that may fall on its surface (Peters 1984). However, we (ECP, CEV, LSG) have observed that during periods of cold weather (in both Rhode Island and Texas corals) the coenosarc tissues of *A. poculata* often contract and expose the coenosteum (as the polyps contract and forego feeding), which may be covered with sediment or colonized by algae. These lesions may contribute to the formation of digitate colonies when the coral resumes skeletal deposition in the spring, although this has not been confirmed ex-

perimentally. St. Pierre (1986) also observed high variability in colony morphology from encrusting to ramose or both types on the same colony, at the Port Aransas jetty. Jaap (in prep.) noted that substratum may also control colony morphology, with encrusting forms found on mollusk fragments or shells and thicker or branching forms on igneous rock bases. As for other skeletal characters, Jaap (in prep.) reported that Gulf of Mexico specimens generally had smaller corallite diameters and there were reduced numbers of septa in specimens taken from Texas or the western Gulf sites. He observed a minimum annual growth rate (basal diameter) of 38.4 to 46.8 mm for two clusters of *Astrangia* which attached to a stone crab trap between April and September 1977 (Jaap, in prep.). The largest branching specimen in the USNM (USNM 78508, Fig. 4) was collected from 263 m depth off Western Dry Rocks, Sand Key, Florida.

The cellular composition and structure of *Astrangia poculata* are distinctive, particularly in the development of the mesogleal pleats and the granules in the cells of the aboral gastrodermis and calicoblast epidermis, and differ from other members of this and closely-related families, such as the Oculinidae (see Peters 1984). *A. poculata* is one of the few subtropical to temperate corals that may possess symbiotic dinoflagellate algae known as zooxanthellae within its gastrodermal tissues, and is the only member of the genus reported to do so. Cummings (1976), Jacques et al. (1977), and Szmant-Froelich (1980a) showed that zooxanthellae densities in some colonies from Narragansett Bay may be equal to or greater than those reported to occur in tropical reef corals. In Narragansett Bay, colonies with zooxanthellae are found directly adjacent to those without, and there are colonies that are only partially pigmented (spotted) brown by the algae. All varieties are found throughout the year. Colonies which appear to lack zooxanthellae usually possess small popu-

lations of the algae (less than 1×10^5 cells per polyp). Hence, Swart's (1983:72) arguments that colonies of *A. danae* (= *A. poculata*) that lack zooxanthellae might be a different species, or might be found under stress conditions, appear to be invalid.

Algal populations do vary seasonally with changes in light intensity and temperature (Cummings 1983), and under sedimentation stress (Peters & Pilson 1985). The algal populations also increase under conditions of high light and temperature in the laboratory (Cummings & McCarty 1982, Cummings 1983, Peters & Pilson 1985). Cummings (1976, 1983) suggested that this change was caused by differences in physiological tolerances between zooxanthellate and azooxanthellate colonies, with the former better adapted to summer (high temperature and light) and the latter better adapted to winter (low temperature and light) conditions. Possibly, because of the seasonal fluctuations of these conditions, fully zooxanthellate colonies are not numerically dominant in Narragansett Bay. Jacques (1978) observed that at high light and temperature conditions, the zooxanthellate colonies calcified significantly faster than azooxanthellate ones. Peters & Pilson (1985) found that the tissues of zooxanthellate colonies were more easily damaged by combined sedimentation and starvation stress than azooxanthellate colonies, and suggested that genetic as well as environmental factors influence the symbiosis. Weston (1980) found only zooxanthellate colonies in the relatively well-illuminated surface waters of Chesapeake Bay and azooxanthellate colonies deeper. Both kinds were found inhabiting a transition zone, the depth of which correlated with 89 to 95% attenuation of surface incident light. He also suggested that both genetic and environmental factors might influence the symbiosis. The colonies which Brunet (1982) found on shallow substrata (less than 2 m water depth) at the Port Aransas, Texas, jetty site contained zooxanthellae. At depths greater than

2 m, and at the oil rig and the Liberty ship, specimens of *Astrangia* always lacked zooxanthellae.

Colonies of *Astrangia poculata* tolerate a wide variety of environmental conditions. In nature, populations have been found in salinities ranging from oceanic (36‰) seawater (Cummings 1976) to salinities of 16–19‰ in Texas bays (Ladd 1951). Experimentally, this coral can adapt to salinities ranging from 10 to 40‰ (Ferguson 1948, Cummings 1976) and can survive for more than six days under low oxygen conditions (Sassaman & Mangum 1973). In Narragansett Bay, Rhode Island, *A. poculata* survives an annual temperature range of -1.5°C to 22°C , and up to 35°C under experimental conditions in the laboratory (Cummings 1976, Jacques 1978, Peters & Pilson 1985). St. Pierre (1986) observed annual temperature fluctuations from 17°C to 30°C during a study of *Astrangia* from Port Aransas, Texas. The unusual hardiness of *A. poculata* is illustrated by the fact that MEQP (unpublished) often kept colonies in small containers in his office. In one case a small colony was maintained for more than three years in a one-liter container, often without feeding it or changing the water for months.

The sexual reproduction of *A. poculata* in Narragansett Bay, Rhode Island, was examined by Szmant-Froelich et al. (1980). They demonstrated that each colony is dioecious, with a 1:1 male : female sex ratio for the population. Fertilization is external, with development of planktonic planula larvae, and zooxanthellae are not passed on in the eggs or sperm but must be acquired after settlement. An annual reproductive cycle appeared to be tied to the seasonal maximum temperature. Well-fed colonies, experimentally maintained year-round under high light and temperature ($20\text{--}22^{\circ}\text{C}$ or 26°C) conditions continuously produced gametes (Szmant-Froelich 1981, Peters & Pilson 1985). St. Pierre (1986) studied the reproductive cycle of a population of *Astrangia* from a jetty off Port Aransas, Texas. She

also found a 1:1 sex ratio. Gametogenesis began in February, with spawning occurring in late August to September, corresponding to the maximum water temperatures at this Gulf of Mexico site. Another cycle of gametogenesis appeared to begin in November. Similarly, a second cycle was reported for the Rhode Island colonies beginning in October. Because the reproductive cycle of this coral appears to be essentially the same throughout its range, St. Pierre supported the synonymy of *A. danae* with *A. astreiformis* (St. Pierre 1986).

Acknowledgments

We thank all of the "Friends of *Astrangia*" whose interest in this coral over the years prompted this work. We are also grateful to C. J. Durden and H. B. McCarty for helpful discussions and manuscript review, and to F. M. Bayer and C. W. Sabrosky for advice on nomenclature leading to the choice of neotype for both *poculata* and *michelinii*. Publication n.s.-3 of the Texas Memorial Museum, University of Texas.

Literature Cited

- Agassiz, A., & E. C. Agassiz. 1865. Sea-side studies in natural history. Boston, 155 pp.
- Agassiz, L. 1850. On the structure of coral animals.—Proceedings of the American Association for the Advancement of Science 2:68–77.
- Allee, W. C. 1923. Studies in marine ecology I. The distribution of common littoral invertebrates of the Woods Hole region.—Biological Bulletin 44(4):167–191.
- Alloiteau, J. 1952. Généralités sur les Coelentérés; Hydrozoaires; Scyphozoaires; Alcyonaires; généralités sur les Madréporaires; Madréporaires post-paléozoïques. Pp. 376–410, 539–684 in J. Piveteau, ed., Traité de paléontologie, Volume 1. Masson, Paris.
- Bachand, R. G. 1978. Cold water coral.—Sea Frontiers 24:283–284.
- Blake, S. F. 1953. The Pleistocene fauna of Wailes bluff and Langleys bluff, Maryland.—Smithsonian Miscellaneous Collections 121(12):1–32.
- Boschma, H. 1925a. The nature of the association between anthozoa and zooxanthellae.—Pro-

- ceedings of the National Academy of Sciences 11:65-67.
- . 1925b. On the feeding reactions and digestion in the coral polyp *Astrangia danae*, with notes on its symbiosis with zooxanthellae.—*Biological Bulletin* 49:407-439.
- Brunet, C. 1982. Coral feeding rates and food resource selectivity in response to various densities of naturally occurring zooplankton. M. S. Thesis, University of Texas at Austin, 150 pp.
- Buchanan, J. B. 1954. The zoogeographical significance of the Madreporaria collected in the Gold Coast, West Africa.—*Revue de Zoologie et de Botanique Africaines* 49(1-2):84-88.
- Cairns, S. D. 1977. Stony corals I. Caryophylliina and Dendrophylliina. *Memoirs of the Hourglass Cruises* [Marine Research Laboratory, Department of Natural Resources, St. Petersburg, Florida] 3(4), 27 pp.
- . 1978. A checklist of the ahermatypic scleractinia of the Gulf of Mexico, with the description of a new species.—*Gulf Research Reports* 6:9-15.
- . 1979. The deep-water scleractinia of the Caribbean Sea and adjacent waters. Studies on the Fauna of Curaçao and Other Caribbean Islands, No. 180, 341 pp.
- . 1981. Marine flora and fauna of the northeastern United States: Scleractinia.—NOAA Technical Report, NMFS Circular 438, U.S. Department of Commerce, 15 pp.
- Calder, D. R. 1972. Phylum Cnidaria. Pp. 97-102 in M. L. Wass et al., compilers, A checklist of the biota of lower Chesapeake Bay. Special Scientific Report No. 65, Virginia Institute of Marine Science.
- , & B. S. Hester. 1978. Phylum Cnidaria. Pp. 87-93 in R. G. Zingmark, ed., An annotated checklist of the biota of the coastal zone of South Carolina. Belle W. Baruch Institute of Marine Biology and Coastal Research, University of South Carolina Press, Columbia, South Carolina.
- Chevalier, J.-P. 1966. Contribution a l'étude des madréporaires des côtes occidentales de l'Afrique tropicale (I^{re} partie).—*Bulletin de l'Institut Français Afrique Noire* 28 (series A):912-975.
- Cooley, N. R. 1978. An inventory of the estuarine fauna in the vicinity of Pensacola, Florida.—*Florida Marine Research Publication* No. 31, 113 pp.
- Courtney, C. M., & T. D. Edmond. 1974. The macroinvertebrates of Marco Island, Florida. Pp. 51-159 in Marco Applied Marine Ecology Station Progress Report, July 1 1974-Dec 31 1974, Marco Island, Florida.
- Cowles, R. P. 1930. A biological study of the offshore waters of Chesapeake Bay.—*Bulletin of the United States Bureau of Fisheries* 46 (for 1931): 277-381.
- Cummings, C. E. 1976. The effects of temperature and salinity on the survival and respiration of *Astrangia danae* with and without zooxanthellae. M. S. Thesis, University of Rhode Island, 115 pp.
- . 1983. The biology of *Astrangia danae* (Milne Edwards & Haime 1849): Studies of biotic and abiotic factors affecting the physiology and morphology of the northern star coral. Ph.D. Dissertation, University of Rhode Island, 147 pp.
- , & H. B. McCarty. 1982. Stable carbon isotope ratios in *Astrangia danae*: evidence for algal modification of carbon pools used in calcification.—*Geochemica et Cosmochimica Acta* 46:1125-1129.
- Damon, W. E. 1882. Coral in an aquarium.—*American Microscopy Journal* 3:221.
- Dana, J. D. 1846. Zoophytes. United States Exploring Expedition (1838-1842), 740 pp.
- . 1872. Coral and coral islands. Dodd and Mead, Publishers, New York, 398 pp.
- . 1890. Corals and coral islands, third edition. Dodd, Mead, and Company, New York, 440 pp.
- Defenbaugh, R. B. 1976. A study of the benthic macroinvertebrates of the continental shelf of the northern Gulf of Mexico. Ph.D. Dissertation, Texas A&M University, 476 pp.
- Driscoll, E. G. 1967. Attached epifauna-substrate relations.—*Limnology and Oceanography* 12:633-641.
- Ellis, J. 1755. An essay towards a natural history of the corallines, and other marine productions of the like kind, commonly found on the coasts of Great Britain and Ireland. London, for the author, 103 pp., 37 [38] pls.
- , & D. Solander. 1786. The natural history of many curious and common zoophytes collected from various parts of the globe. Benjamin White and Son, London, 206 pp.
- Esper, J. C. 1790. Die Planzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen, volume 1, parts 5-6:193-320.
- Ferguson, A. H. 1948. Experiments on the tolerance of several marine invertebrates to reduced salinity.—*Proceedings of the Louisiana Academy of Science* 11:16-17.
- Fewkes, J. W. 1889. The anatomy of *Astrangia danae*.—Six lithographs from drawings by A. Sonrel. Natural history illustrations prepared under the direction of L. Agassiz, 1849. Explanation of plates by Fewkes. Published by the Smithsonian Institution, 20 pp.
- . 1891. An aid to a collector of the Coelenterata and Echinodermata of New England.—*Bulletin of the Essex Institute* 23:1-92.

- Field, L. R. 1949. Sea anemones and corals of Beaufort, North Carolina.—Bulletin of Duke University Marine Station, Durham, North Carolina, No. 5:1–39.
- Foster, A. B. 1979. Phenotypic plasticity in the reef corals *Montastraea annularis* (Ellis & Solander) and *Siderastrea sidera* (Ellis & Solander).—Journal of Experimental Marine Biology and Ecology 39:250–254.
- . 1980. Environmental variation in skeletal morphology within the Caribbean reef corals *Montastraea annularis* and *Siderastrea sidera*.—Bulletin of Marine Science 30:678–709.
- Fotheringham, N., & S. L. Brunenmeister. 1975. Common marine invertebrates of the northwestern Gulf coast. Gulf Publishing Company, Houston, Texas, 197 pp.
- , ———, & P. Mcnefee. 1980. Beachcomber's guide to Gulf coast marine life. Lone Star Books, Houston, Texas, 124 pp.
- Gmélín, J. F. 1791. Carolus Linne Systema Naturae. Leipzig, edition 13, 1(6):3021–3910.
- Goreau, T. F., & V. T. Bowen. 1955. Calcium uptake by a coral.—Science 122:1188–1189.
- , N. I. Goreau, & C. M. Yonge. 1971. Reef corals: autotrophs or heterotrophs.—Biological Bulletin 141:247–260.
- Gosner, K. L. 1979. A field guide to the Atlantic seashore. Houghton Mifflin Company, Boston, 329 pp.
- Gunter, G., & R. A. Geyer. 1955. Studies on fouling organisms of the northwest Gulf of Mexico.—Publications of the Institute of Marine Science 4:39–67.
- Hand, C. 1964. Phylum Cnidaria. Pp. 25–28 in R. I. Smith, ed., Keys to marine invertebrate faunas of the Woods Hole region. Contribution No. 11 Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Massachusetts.
- Hargitt, C. W. 1914. The Anthozoa of the Woods Hole region.—Bulletin of the United States Bureau of Fisheries 32(for 1912):223–254 (Document No. 788).
- Hayes, R. L., & N. I. Goreau. 1977. Intracellular crystal-bearing vesicles in the epidermis of scleractinian corals, *Astrangia danae* (Agassiz) and *Porites porites* (Pallas).—Biological Bulletin 152: 26–40.
- Hedgpeth, J. 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna.—Publications of the Institute of Marine Science 3:111–224.
- Hoffman, R. J., S. H. Bishop, & C. Sassaman. 1978. Glutamate dehydrogenase from coelenterates NADP specific.—Journal of Experimental Zoology 203:165–170.
- Hyman, L. H. 1940. The invertebrates: protozoa through Ctenophora. McGraw-Hill, New York, 726 pp.
- International Code of Zoological Nomenclature. 1985. H. Charlesworth and Company, Limited, Huddersfield, England, 338 pp.
- Jaap, W. C. (in prep). Stony corals II. Memoirs of the Hourglass Cruises. [Marine Research Laboratory, Department of Natural Resources, St. Petersburg, Florida.]
- Jacques, T. G. 1978. Metabolism and calcification of the temperate scleractinian coral *Astrangia danae*. Ph.D. Dissertation, University of Rhode Island, 169 pp.
- , & M. E. Q. Pilson. 1980. Experimental ecology of the temperate scleractinian coral *Astrangia danae*. I. Partition of respiration, photosynthesis and calcification between host and symbionts.—Marine Biology Berlin 60:167–178.
- , N. Marshall, & M. E. Q. Pilson. 1983. Experimental ecology of the temperate scleractinian coral *Astrangia danae*. II. Effect of temperature, light intensity and symbiosis with zooxanthellae on metabolic rate and calcification.—Marine Biology Berlin 76:135–148.
- , M. E. Q. Pilson, C. E. Cummings, & N. Marshall. 1977. Laboratory observations on respiration, photosynthesis, and factors affecting calcification in the temperate coral *Astrangia danae*.—Proceedings of the Third International Coral Reef Symposium 2:455–461.
- Keith, M. L., & J. N. Weber. 1965. Systematic relationships between carbon and oxygen isotopes in carbonates deposited by modern corals and algae.—Science 150:498–501.
- Ladd, H. S. 1951. Brackish-water and marine assemblages of the Texas coast, with special reference to molluscs.—Publications of the Institute of Marine Science 2(1):125–164.
- Lang, J. C. 1984. Whatever works: the variable importance of skeletal and of non-skeletal characters in scleractinian taxonomy.—Paleontographica Americana 54:18–44.
- Leidy, J. 1855. Contributions towards knowledge of the marine invertebrate fauna of the coasts of Rhode Island and New Jersey.—Journal of the Academy of Natural Science of Philadelphia, 3 (second series):135–152.
- Macintyre, I. G. 1970. New data on the occurrence of tropical reef corals on the North Carolina continental shelf.—Journal of the Elisha Mitchell Scientific Society 86:178 (abstract).
- , & O. H. Pilkey. 1969. Tropical reef corals: Tolerance of low temperatures on the North Carolina shelf.—Science 166:374–375.
- Meinkoth, N. A. 1981. The Audubon Society field guide to North American seashore creatures. Alfred A. Knopf, New York, 798 pp.
- Milne Edwards, H., & J. Haime. 1848a. Note sur la

- classification de la deuxième tribu de la famille des Astréides.—Comptes Rendus, Académie des Sciences Paris 27:490–497.
- & ———. 1848b. Recherches sur les polypiers. Mémoire 4. Monographie des Astréides.—Annales des Sciences Naturelles Zoologie et Paléontologie (Series 3) 10:209–321.
- & ———. 1849. Recherches sur les polypiers. Mémoire 4. Monographie des Astréides.—Annales des Sciences Naturelles Zoologie et Paléontologie (Series 3) 12:95–197.
- , & ———. 1850. A monograph of the British fossil corals, part 1, Introduction. Palaeontographical Society, London, pp. i–lxxxv.
- , & ———. 1857. Histoire naturelle des coralliaires ou polypes proprement dits. Tome 2, À la Librairie Encyclopédique de Roret, 633 pp.
- Pallas, P. S. 1766. Elenchus Zoophytorum. Hagae Comitum, 451 pp.
- Pampe, W. R. 1971. A new Pleistocene marine fossil locality in Chambers County, Texas.—Transactions of the Gulf Coast Association of Geological Societies 21:395–410.
- Parker, R. H. 1956. Macro-invertebrate assemblages as indicators of sedimentary environments in east Mississippi Delta region.—Bulletin of the American Association of Petroleum Geologists 40:295–376.
- . 1959. Macro-invertebrate assemblages of Central Texas coastal bays and Laguna Madre.—Bulletin of American Association of Petroleum Geologists 43(9):2100–2166.
- . 1960. Ecology and distributional patterns of marine macroinvertebrates, northern Gulf of Mexico. Pp. 302–337 in F. P. Shepard et al., eds., Recent sediments, Northwest Gulf of Mexico. American Association of Petroleum Geologists, Tulsa.
- Pearse, A. S. 1936. Estuarine animals at Beaufort, North Carolina.—Journal of the Elisha Mitchell Scientific Society 52(2):174–222.
- , & G. W. Wharton. 1938. The oyster “leech” *Stylochus inimicus* Palombi associated with oysters in the coasts of Florida.—Ecological Monographs 8:605–655.
- , & G. Williams. 1951. The biota of the reefs off the Carolinas.—Journal of the Elisha Mitchell Scientific Society 67:133–161.
- Peters, E. C. 1984. A survey of the normal and pathological histology of scleractinian corals with emphasis on the effects of sedimentation stress. Ph. D. Dissertation, University of Rhode Island, 283 pp.
- , & M. E. Q. Pilson. 1985. A comparative study of the effects of sedimentation on symbiotic and asymbiotic colonies of the coral *Asrangia danae* Milne Edwards and Haime 1849.—Journal of Experimental Marine Biology and Ecology 92:215–230.
- Pilson, M. E. Q. 1975. The genus *Asrangia*: Notes, list of species, and an annotated bibliography. Unpub. ms.
- Pourtales, L. F. 1871. Deep sea corals. Illustrated catalogue of the Museum of Comparative Zoology at Harvard College, No. IV. Cambridge, Printed for the Museum of Comparative Zoology, 93 pp., 8 pls.
- Pratt, H. S. 1935. A manual of the common invertebrate animals (Revised edition), McGraw-Hill Co., New York, 854 pp.
- Rabalais, S. C. 1978. Fouling communities of selected artificial substrates in the northwestern Gulf of Mexico. M. S. Thesis, Texas A&I University, 99 pp.
- Richards, H. G., & A. Harbison. 1942. Miocene invertebrate fauna of New Jersey.—Proceedings of the Academy of Natural Sciences of Philadelphia 94:167–250.
- Richmond, E. A. 1962. The fauna and flora of Horn Island, Mississippi. Gulf Research Reports 1: 59–106.
- Robertson, R., R. S. Scheltema, & F. W. Adams. 1970. The feeding, larval dispersal, and metamorphosis of *Phillipa* (Gastropoda, Architectoniciidae).—Pacific Science 24:55–65.
- Rudloe, J. 1971. The erotic ocean. World Publishing, New York, 448 pp.
- St. Pierre, L. J. 1986. Gametogenesis of the warm water coral *Asrangia astreiformis* (Anthozoa: Scleractinia). M.S. Thesis, Texas A&M University, 55 pp.
- Sassaman, C., & C. P. Mangum. 1973. Relationship between aerobic and anaerobic metabolism in estuarine anemones.—Comparative Biochemistry and Physiology 44A:1313–1319.
- Schuhmacher, H., & H. Zibrowius. 1985. What is hermatypic? A redefinition of ecological groups in corals and other organisms.—Coral Reefs 4: 1–9.
- Seba, A. 1758. Locupletissimi rerum naturalium thesauri accurata descriptio, et iconibus artificiosissimus expressio per universam physices historium. . . . Amstelae dami, volume 3.
- Stephenson, T. A., & A. Stephenson. 1952. Life between tidemarks in North America II. Northern Florida and the Carolinas.—Journal of Ecology 40:1–49.
- Storer, T. I. 1951. General zoology. McGraw-Hill Book Company, New York, 832 pp.
- , R. L. Usinger, R. C. Stebbins, & J. W. Nybakken. 1979. General zoology. 6th ed., McGraw-Hill Book Company, New York, 902 pp.
- Swart, P. K. 1983. Carbon and oxygen isotope frac-

- tionation in scleractinian corals: a review.—*Earth-Science Reviews* 19:51–80.
- Szmant-Froelich, A. 1980a. Studies of the reproduction, nutrition and symbiosis with zooxanthellae of the temperate scleractinian coral *Astrangia danae*. Ph.D. Dissertation, University of Rhode Island, 191 pp.
- . 1980b. The coral that lives in Narragansett Bay.—*Maritimes* 24(2):1–3.
- . 1981. Coral nutrition: comparison of the fate of ^{14}C from ingested labeled brine shrimp and from the uptake of $\text{NaH}^{14}\text{CO}_3$ by its zooxanthellae.—*Journal of Experimental Marine Biology and Ecology* 55:133–144.
- , & M. E. Q. Pilson. 1977. Nitrogen excretion by colonies of the temperate coral *Astrangia danae* with and without zooxanthellae.—*Proceedings of the Third International Coral Reef Symposium* 2:417–424.
- , & ———. 1980. The effects of feeding frequency and symbiosis with zooxanthellae on the biochemical composition of *Astrangia danae* Milne Edwards & Haime 1849.—*Journal of Experimental Marine Biology and Ecology* 48:85–97.
- , & ———. 1984. Effects of feeding frequency and symbiosis with zooxanthellae on nitrogen metabolism and respiration of the coral *Astrangia danae*.—*Marine Biology Berlin* 81(2):153–162.
- , P. Yevich, & M. E. Q. Pilson. 1980. Gametogenesis and early development of the temperate coral *Astrangia danae* (Anthozoa: Scleractinia).—*Biological Bulletin* 158:257–269.
- Thiel, M. E. 1928. Madreporaria. In J. W. Michaelson, ed., *Beitrage zur Kenntnis der Meeresfauna Westafrikas* 3:251–350.
- . 1941. Résultats scientifiques des Croisières du Navire-Edole belge "Mercator." Vol. III, 1. Madreporaria.—*Mémoires du Musée Royal d'Histoire Naturelle de Belgique* (2) 21:3–28, 3 pls, i–iii.
- Turton, W. 1806. A general system of nature through the three grand kingdoms . . . by Sir Charles Linne, Vol. IV. Lackington, Allen, and Company, London, pp. 1–727, 2 pls.
- Vaughan, T. W. 1901. The stony corals of the Puerto Rican waters.—*Bulletin of the United States Fish Commission* 20(pt 2):289–320.
- , & J. W. Wells. 1943. A revision of the suborders, families and genera of the Scleractinia.—*Geological Society of America Special Papers* 44:1–363.
- Veron, J. E. 1982. The species concept in Scleractinia of Eastern Australia.—*Proceedings of the Fourth International Coral Reef Symposium* 2:183–186.
- Verrill, A. E. 1863. Revision of the polypi of the eastern coast of the United States.—*Memoirs of the Boston Society of Natural History* 1:1–45.
- . 1864. List of the polyps and corals sent by the Museum of Comparative Zoology to the other institutions in exchange, with annotations.—*Bulletin of the Museum of Comparative Zoology* 1:29–60.
- . 1866a. On the polyps and corals of Panama with descriptions of new species.—*Proceedings of the Boston Society of Natural History* 10:323–333.
- . 1866b. On the polyps and echinoderms of New England, with description of new species.—*Proceedings of the Boston Society of Natural History* 10:333–357.
- . 1872. Brief contributions to zoology from the Museum of Yale College. No. XXII. On the radiata from the coast of North Carolina.—*American Journal of Science and Arts* 3:432–438.
- . 1873. Report on the invertebrate animals of Vineyard Sound and adjacent waters with an account of the physical characters of the region.—*United States Fish Commission Report* 1871–1872, VIII:295–537.
- . 1874. Report upon the invertebrate animals of Vineyard Sound and adjacent waters. Washington, D.C., 478 pp.
- Waterman, T. H. 1950. *Astrangia danae*. Pp. 127–131 in F. A. Brown, ed., *Selected invertebrate types*. John Wiley & Sons, Inc., New York.
- Wells, H. W., M. J. Wells, & I. E. Gray. 1964. The calico scallop community in North Carolina.—*Bulletin of Marine Science* 14:561–593.
- Wells, J. W. 1956. Scleractinia. Pp. F328–F444 in R. C. Moore, ed., *Treatise on invertebrate paleontology*, Part F. Geological Society of America, New York.
- . 1986. A list of scleractinian generic and subgeneric taxa, 1758–1985. *International Association for the Study of Fossil Cnidaria*, volume 15, no. 11, 69 pp.
- Weston, M. P. 1980. Distribution of the dinoflagellate symbiosis in *Astrangia danae* as affected by light attenuation. M.S. Thesis, Old Dominion University, 93 pp.
- Whitten, H. L., H. F. Rosene, & J. W. Hedgpeth. 1950. The invertebrate fauna of Texas coast jetties; a preliminary survey.—*Publications of the Institute of Marine Science* 1:53–87.
- Wijsman-Best, M. 1974. Habitat-induced modification of reef corals (Faviidae) and its consequences for taxonomy.—*Proceedings of the Second International Coral Reef Symposium* 2:217–228.
- Williams, R. B., & M. B. Murdoch. 1973. Effects of

- continuous low-level gamma radiation on sessile marine invertebrates. Pp. 1-786 in Anonymous, ed., Radioactive contamination of the marine environment. International Atomic Energy Agency, Vienna.
- Wilson, H. V. 1900. Marine biology at Beaufort.—*American Naturalist* 34(401):339-360.
- Wiseman, R. W. 1984. Light intensity effects on superoxide dismutase activity in symbiotic colonies of *Astrangia danae*. M.S. Thesis, University of Rhode Island, 75 pp.
- Zibrowius, H. 1980. Les scléactiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Mémoires de l'Institut Oceanographique Monaco*, no. 11, 284 pp.
- Zinn, D. J. 1964. Yes, there are corals in Rhode Island.—*Maritimes* 8(4):15-16.
- (ECP)(SDC) Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; (MEQP) Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island 02882-1197; (JWW) Department of Geological Sciences, Cornell University, Ithaca, New York 14853-1504; (WCJ) Florida Department of Natural Resources, Bureau of Marine Research, 100 Eighth Avenue S.E., St. Petersburg, Florida 33701; (JCL) Texas Memorial Museum, University of Texas, Austin, Texas 78705, and Department of Zoology, University of Texas, Austin, Texas 78712; (CEV) Amoco, 200 East Randolph Drive, Chicago, Illinois 60601; (LSG) Biology Department, Texas A&M University, College Station, Texas 77843.